
Guadua chacoensis (Poaceae: Bambuseae), its Taxonomic Identity, Morphology, and Affinities

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ABSTRACT. A new combination, *Guadua chacoensis*, is made. Based on morphological evidence, *G. chacoensis* appears closely allied to *G. trinii*. A detailed illustration of the species is included, and morphological descriptions and illustrations of the seedling and fruit are provided.

Guadua was segregated from the genus *Bambusa* Schreber and described by Kunth (1822). Important diagnostic characters that distinguish this genus are triangular culm leaves in which the margins of the sheath and blade are usually contiguous, a distinctive band of short white hairs above and below the nodal line, synflorescences with 2- to many-flowered pseudospikelets, a palea of firm texture with prominent wings emanating from the keels, and the presence of stomata and papillae on the adaxial surface of the leaf blades (Soderstrom & Ellis, 1987; Soderstrom & Londoño, 1987). Other characters useful in distinguishing among the species of the genus are the shape of culm and foliage leaf, the structure and shape of pseudospikelets, and the habit of the plant.

Guadua occurs throughout tropical America, from Mexico to northern Argentina, and contains perhaps 30 species. Along with *Guadua*, four other genera are placed in the subtribe Guaduinae: *Criciuma* Soderstrom & Londoño and *Eremocaulon* Soderstrom & Londoño from Brazil, and *Olmeca* Soderstrom and *Otatea* (McClure & Smith) Calderón & Soderstrom, from Mexico (Soderstrom & Ellis, 1987).

Guadua chacoensis occurs in northern Argentina, southeastern Bolivia, and southern Paraguay and is one of the three southeasternmost species of the genus. It is frequently misidentified as *G. angustifolia* Kunth. The species was described in 1918 by the Argentinian botanist Nicolas Rojas Acosta as *Bambusa chacoensis*. A type specimen was not designated but the locality data (General Vedia, Depto. Bermejo, Prov. del Chaco-Argentina, and Ile de la Colonia Aquino, Río Paraguay) and the common

name "tacuara," distinguish it from two species that occur sympatrically, *G. paraguayana* Doell, "picanilla," and *Guadua trinii* (Nees) Ruprecht, "yatevó," "tacuaruzú," or "tacuara brava" (Nicora & Rógolo, 1987; Young, 1985).

McClure (1973), in his annotated checklist of species, included *G. chacoensis* under the heading of unresolved specific taxa. Young (1985) treated this species as one of two subspecies in the variable *Guadua angustifolia* Kunth complex and indicated a neotype. However, Young (1985) pointed out that "the two subspecies can be separated using a combination of vegetative and reproductive characters but since the morphological gap separating them is smaller than that separating most species in the subgenus, the taxa are considered here to be only subspecifically distinct."

In this study, a comparison of floral and vegetative morphology among *G. chacoensis*, *G. angustifolia*, and *G. trinii* is presented. Based on complete material collected by Camilo Quarín, a botanist from the Universidad Nacional del Nordeste, Corrientes, Argentina, a detailed illustration of the habit of *G. chacoensis* and descriptions and illustrations of the seedling and fruit are provided.

Guadua chacoensis (Rojas) Londoño & Peterson, comb. nov. Basionym: *Bambusa chacoensis* Rojas, Bull. Acad. Int. Géogr. Bot. 26: 157. 1918. TYPE: Argentina. Chaco: Departamento Bermejo, General Vedia, Riberas del Río de Oro, 23 July 1974, Quarín et al. 2384 (neotype, designated here, CTES; isoneotypes, F, G not seen, MO, US). Figure 1.

Woody, thorny bamboo. *Rhizomes* pachymorph. *Culms* 10–20 m tall, 8–15 cm diam., green, erect below and arching apically; *internodes* hollow; *nodes* solitary; *bud* solitary, covered by a prophyll, positioned 2–4 mm above the nodal line. *Culm leaves*



Figure 1. *Guadua chacoensis* (Rojas) Londoño & Peterson. —A. Flowering branch. —B. Leaf complement. —C. Leaf ligule. —D. Culm sheath. —E. Detail of culm sheath ligule, adaxial view. —F. Branch complement. Based on: A, *Quarin et al.* 2384; B, C, *Schinnini* 10956; D, *Tressencs & Schinnini* 1310; E, F, *Schinnini et al.* 6819.

coriaceous, light brown to stramineous, deciduous, the blade $\frac{1}{3}$ – $\frac{1}{4}$ as large as the sheath; *sheath* 20–50 cm long, 8–30 cm wide, abaxially strigose to glabrescent, the coarse, rigid, brown hairs to 2 mm long, easily removed, adaxially glabrous, shiny, and tessellate, auricles and fimbriae absent; *blade* 4–13 cm long, 3–8 cm wide, triangular, erect, persistent, strongly mucronate at the apex, abaxially strigose to glabrous, adaxially conspicuously nerved and pubescent between the nerves, the margins ciliate with hyaline, deciduous hairs, up to 2.5 mm long, the junction with the sheath slightly curved to \pm horizontal; *inner ligule* 0.8–1 mm long, glabrous, stramineous, ciliate along the margin, following the junction between the sheath and the blade and ending at the margins; *outer ligule* absent. *Branching* intravaginal; primary branch solitary and armed, later developing 2 or 3 secondary branches from the basal proximal nodes. *Foliage leaves* 7 to 9 per complement; *sheath* glabrous, nonauriculate, ciliate on the margins; fimbriae 2–3 mm long, restricted to the sheath summit, erect basally, wavy to curly distally, 3–5 per tuft, white-ivory; *blade* 10–24 cm long, 0.5–2.5 cm wide, L:W ratio 11–26:1, extremely variable in size, linear, 8–14-nerved, adaxially glabrous to sparsely hispid, the hairs 0.5–1 mm long, hyaline to brown, antrorse, 3–4 rows of prickly-hairs along one margin, abaxially glabrous, with sparsely coarse, rigid, hyaline hairs mainly along the midnerve, the margins strigose; *pseudopetiole* 2–3 mm long, adaxially pilose to glabrous, abaxially glabrous; *inner ligule* 0.2–0.4 mm long, minutely pubescent, ciliate on the margin with erect, hyaline hairs, the hairs 0.2 mm long; *outer ligule* 0.1–0.2 mm long, minutely ciliate on the margin. *Synflorescence* 30–40(–50) cm long, usually terminating leafless branches, consisting of 6–9 cincinni with 4–7 multiflowered pseudospikelets per cincinnus; rachis glabrous. *Pseudospikelet* 2–5(–6) cm long, 0.4–0.5(–0.6) cm wide, robust and erect, straight, corpulent, green when young, later brown to stramineous, consisting of a subtending bract, a prophyll, 1–2 glumes, 1–2 sterile lemmas, 2–4(–6) fertile florets, in a terminal rudimentary anthecium; *rachilla* 5–7 mm long between florets, hispidulous; *subtending bracts* 8–10 mm long, 4–5 mm wide, ovate to ovate-lanceolate, abaxially glabrous to sparsely pubescent, adaxially minutely pubescent on the distal $\frac{1}{3}$, the apex mucronate; *prophyll* winged, pubescent between keels and ciliate on the wings, occasionally gemmiferous; *glumes* 5–8 mm long, 3 mm wide, 1–2, usually gemmiferous, broadly ovate to ovate-lanceolate, 7–9-nerved, mucronate, positioned close to the prophyll, abaxially shiny, with scattered minute transparent hairs on the dorsal

part, adaxially minutely pubescent, with transverse venations apically, the margins smooth; *sterile lemma* 10–14 mm long, 6–10 mm wide, sometimes enclosing a rudimentary palea, usually stramineous, mucronate, abaxially shiny and glabrous, adaxially minutely pubescent, the margins scarious, smooth; *fertile lemma* 12–16 mm long, 7–12 mm wide, ovate-lanceolate, 12–17-nerved, totally embracing the palea, mucronate, stramineous or purplish, abaxially covered with hyaline, appressed, sometimes spreading hairs on the proximal $\frac{1}{2}$, otherwise glabrous and shiny, adaxially shiny, minutely pubescent, the margins scarious, shiny, bearing a tuft of hairs distally, below the mucro, the mucro 0.8–1 mm long, brown when old; *palea* 6–14 mm long, 2–4 mm wide, usually shorter than the lemma, stramineous, abaxially pubescent, adaxially glabrous, the sulcus 2–2.5 mm wide, 3-nerved, apiculate at the apex with a tuft of hairs, the keels winged, the wings 1–1.5 mm long, 2–3-nerved, stramineous, prolonged at the apex, ciliate on the margin, abaxially puberulous close to the keels, otherwise glabrous and shiny, adaxially glabrous, the enfolded margins 3-nerved, glabrous. *Lodicules* 3, transparent, many-nerved, glabrous, ciliate on the upper part of the margin; the anterior pair 3–5 mm long, 2–3 mm wide, the posterior one 2–3 mm long, 1.5–2 mm wide. *Stamens* 6; anthers 5–8 mm long, 0.5–1 mm wide, sagittate at the base, apiculate at the apex of each theca, yellowish brown. *Ovary* 2–4 mm long, 1–2 mm wide, fusiform, glabrous and shiny; style 2–3 mm long, hispidulous, darker than the ovary with 3 plumose stigmas, the stigmas 3 mm long and purple when young. *Fruit* 9–12 mm long, 2.5–5 mm wide, an asymmetric fusiform caryopsis, brown, glabrous; embryo 2–3 mm long, 2–3 mm wide, basal, circular.

Distribution. Known from northern Argentina, southeastern Bolivia, and southern Paraguay where it occurs in gallery forests usually along stream and river edges at elevations of 75–450 m.

Additional specimens examined. ARGENTINA. CORRIENTES: Depto. Capital, Arroyo Riachuelo y Ruta 12, 16 Jan. 1974 (fl), *Quarin et al.* 1859 (US), 15 Aug. 1974 (fl), *Quarin* 2402 (MO, US); 21 Dec. 1974 (fl), *Maruñak* 635 (US); 27 Nov. 1975 (fl), *Quarin* 3125 (MO, US); Puente Pesoa, Arroyo Riachuelo, 3 Aug. 1973, *Schinnini et al.* 6819 (US); Depto. Concepción, Rincón de San Pedro, 17 Dec. 1974 (fl), *Burkart et al.* 30687 (MO, US), *Quarin* 2870 (MO, US); Depto. Empedrado, Ruta 12 y Río Empedrado, 24 Oct. 1975 (fl), *Quarin* 3210 (MO, US); Depto. Ituzaingó, Isla Apipé Grande, Pto. San Antonio, 8 Dec. 1974 (fl), *Krapovickas et al.* 23851 (MO, US); Rincón Ombu Chico, 4 July 1974 (fl), *Krapovickas et al.* 25470 (MO, US); Depto. Mercedes, 75 km N de Mercedes, Laguna Trin, 17–24 Oct. 1975 (fl),

Quarin et al. 3182 (US). MISIONES: vicinity of Pto. Aguirre, 100 m, 8–10 July 1914, *Curran* 676 (F, NY, US); Pto. León, 75–100 m, 21 July 1914 (fl), *Curran* 677 (NY, US); Iguazú, 7 Oct. 1910, *Rodriguez* 486 (MO, NY, US); San Ignacio, Peñon Reina Victoria, 14 Jan. 1976 (fl), *Krapovickas & Cristóbal* 28759 (MO, US). CHACO: Depto. Bermejo, Isla Guascará, 2 July 1981, *Tressens & Schinnini* 1310 (US); Casa lata, 28 July 1944 (fl), *Rojas* 11719 (NY). TUCUMÁN: Cultivado, Jardines Instituto Miguel Lillo, procedente de Misiones, Iguazú, 26 Aug. 1976 (fl), *Cuezzo s.n.* (US). BOLIVIA. SANTA CRUZ: Prov. Sara, Río Surutú, 1 Oct. 1925 (fl), *Steinbach* 7233a (F, MO, US); Prov. Ichilo, 15 km SE of Buena Vista, 375 m, 28 July 1987, *Nee et al.* 35397 (MO, NY); Parque Nacional Amboró, along Río Cheyo, 400 m, 24 ago. 1985 (fl), *Solomon* 14021 (MO, US.); 23 km S of Buena Vista along Río Chonta, 420 m, 18 Nov. 1988 (fl), *Nee* 36861 (NY); along Río Saguay, 1.5–3 km NE of entrance into first Andean foothills, 17°38'–39'S, 63°43'W, 375 m, 21 Dec. 1988 (fl), *Nee* 37301 (MO). PARAGUAY. CENTRAL: Ruta 2 y Arroyo Mboiy, 2 Mar. 1975 (fl), *Schinnini* 10956 (US). PARAGUARÍ: sur le bord des ruisseaux, Dec. 1883 (fl), *Balansa* 4346 (P, US). SAN PEDRO: Colonia Nueva Germania, 23 Oct. 1916 (fl), *Rojas* 2311 (US); alto Paraguay, Primavera, 16 June 1957, *Woolston G-112* (NY). CAAGUAZÚ: Orillas arroyo Tebicuary, entre Coronel Oviedo y Colonia Independencia, 15 Oct. 1951 (fl), *Burkart* 18741 (SI, US). ÑEEMBUCÚ: Barranca selvática del río Tebicuary–guazú, Jan. 1944 (fl), *Pavetti & Rojas* 10959 (US).

Flowering. The incidence of flowering and fruiting in bamboos varies from one species to another (McClure, 1966), and according to records of specimens available at F, ISC, MO, NY, and US, *G. chacoensis* flowered in the following years: 1883, 1914, 1925, 1944, 1951, 1957, 1975–1976, 1981, and 1985–1988. We cannot establish a regular flowering cycle for this species; however, it is evident that after a long period without flowering, *G. chacoensis* can flower uninterruptedly for at least 3 years. Observations made by Quarin during 1974–1975 indicated that the flowering culms in *G. chacoensis* are usually leafless, and fruits and seedlings are produced when most of the plant is dry.

The flowering cycle of *G. trinii* appears to be unique and well known in the genus (McClure, 1966). It was reported by Parodi (1955), who personally observed the flowering cycle from the same hereditary line for a period of 30 years (1923–1953). After flowering and fruiting uninterruptedly for one year, the clump died completely (i.e., truly monocarpic). The fruits then fell to the ground and germinated.

The flowering cycle of *G. angustifolia* has not been established yet; however, observations of the flowering cycle of natural stands in Valle del Cauca and Quindío, Colombia, have been made by the first author every year from 1979 to the present. Not all the culms in a single clump flowered, and the

flowering culms remain green or yellowish and continue to produce new foliage leaves. According to McClure (1966), a plant of *G. angustifolia* from Milagro, Ecuador, established under his direction at Chocolá, Guatemala, and Tingo Maria, Peru, had flowered annually during the dry season.

Fruit. The fruits of *G. chacoensis* fall on the ground, germinate, and grow beneath the parent plants. This suggests that the rate of survival of the seeds of *G. chacoensis* is higher than in other species of the genus, such as *G. angustifolia*, where it is comparably low (estimated at less than 1%). In *G. angustifolia*, the young ovary is often destroyed by insects.

Mature fruits of *G. chacoensis* are usually found in the middle section of the pseudospikelet and fall with the rachilla, lemma, and palea attached to the base. The caryopsis is asymmetrical and flattened on one side with a short prolonged, hirsutulous style that persists at the apex (Fig. 2S–2U). The dorsal surface of the fruit has a conspicuous hilum about as long as the fruit (Fig. 2U), and the ventral surface has a prominent embryotegium or covering at the base (Fig. 2T). A cross section of the fruit of *G. chacoensis* reveals the presence of a pericarp, endosperm, and embryo. The pericarp is thin, brown, and approximately 0.1 mm thick, whereas the endosperm is starchy, well developed, creamy-white, and occupies almost the whole diameter of the fruit (Fig. 2T). The embryo is $\frac{1}{4}$ – $\frac{1}{2}$ the length of the whole fruit, cream-yellowish, and is located at the base of the fruit in a lateral position (Fig. 2T).

Upon germination of the embryo, the primary shoot is first to emerge laterally just above and adjacent to the root, and there is no internode between the caryopsis and the coleoptile. The primary shoot is a segmented axis of clearly positive phototropism and bears a foliar appendage at each node. The root grows sinuously downward, 12–15 cm, bearing many secondary adventitious roots throughout (Fig. 2W).

The seedling of *G. chacoensis* consists of, from the base upward, a coleoptile, the first basal culm leaf sheath with an elongated internode, the second basal culm leaf sheath with another elongated internode, followed by one culm leaf sheath with a broad, ovate-lanceolate blade positioned horizontally, one or several blades that develop into the first seedling leaf, and the terminal shoot (Fig. 2V). This morphological pattern seems to represent the developmental sequence of a typical bambusoid seedling (Calderón & Soderstrom, 1973).

Affinities. *Guadua chacoensis* appears to be most closely related to *G. trinii*, rather than *G. angustifolia*. However, in all three species the general

TABLE 1. A selective morphological comparison of *Guadua chacoensis*, *G. trinii*, and *G. angustifolia*.

Character	<i>G. chacoensis</i>	<i>G. trinii</i>	<i>G. angustifolia</i>
Culm leaf			
inner ligule	slightly curved and ending at the margins	more or less horizontal and ending at the margins	convex and ending before the margins
Foliage leaf			
blade size (cm)	10–24 × 0.5–2.5	4.5–11 × 0.4–1.3	11–21 × 1–2
l:w ratio	11–26:1	7–12:1	5–18:1
form	linear	linear	linear to lanceolate-ovate
Pseudopetiole			
length (mm)	2–3	1–2	2–5
adaxial surface	pilose to glabrous	pilose	short pubescent
abaxial surface	glabrous	pilose	glabrous
Pseudospikelet			
size l × w (mm)	2–6 × 0.4–0.6	1.8–4 × 0.4–0.6	4–10 × 0.3–0.4
form	robust and erect	robust and erect	slender and acute
Fertile lemma			
size l × w (mm)	12–16 × 7–12	9–12 × 5–7	9–10 × 5–6
margins	scarious, hairs at the distal end	papery, glabrous distally	papery, glabrous distally
mucro length (mm)	0.8–1	0.5–1	0.5
Palea			
size l × w (mm)	6–14 × 2–4	9–11 × 3	7 × 1–1.5
wing width (mm)	1–1.5	0.5	0.5
apex	prolongated	prolongated	not prolonged
Stamens			
length (mm)	5–8	5–7	4–5
apex	apiculate	apiculate	obtuse

form of the culm leaves, foliage leaves, and habit are similar.

Guadua chacoensis and *G. trinii* share the following characters: (1) a more or less horizontal junction between the culm blade and sheath; (2) a culm leaf inner ligule ending at the margins (Fig. 1D); (3) erect and robust pseudospikelets (Figs. 1A, 2A); (4) prolongation of the keels-winged at the apex; and (5) a monocarpic habit, commonly with a leafless flowering branch. *Guadua chacoensis* differs from *G. trinii* by having abaxially glabrous pseudopetioles, longer (10–24 cm) leaf blades that are generally wider (0.5–2.5 cm), and a lemma that is longer than the palea (Table 1).

Guadua chacoensis can be distinguished from *G. angustifolia* by having: (1) a slightly curved and continuous inner ligule ending at the margins; (2) a glabrous leaf sheath (Fig. 1C); (3) a conspicuously ciliate margin of the inner ligule of the foliage leaf

(Fig. 1C); (4) an adaxially pilose to glabrous pseudopetiole; (5) erect and robust pseudospikelets; (6) a scarious margined lemma, with a tuft of hairs at the apex (Fig. 2I); (7) a prolongation of the keeled wings at the apex of the palea; (8) apiculate apex of each anther theca (Fig. 2P); (9) an asymmetrical, fusiform caryopsis (Fig. 2S); and (10) monocarpic, leafless flowering culms (Table 1). The geographic distribution of *G. chacoensis* is completely allopatric with that of *G. angustifolia*, which occurs in northwestern South America and Panama.

Acknowledgments. We are grateful to José Cuatrecasas, Emmet Judziewicz, Lynn Clark, and Lars Peter Kvist for advice and support during this study. Special thanks are given to Alice R. Tangerini for her skillful illustrations. Support for the first author was provided by a Smithsonian Institution Short-Term Visitor Grant.

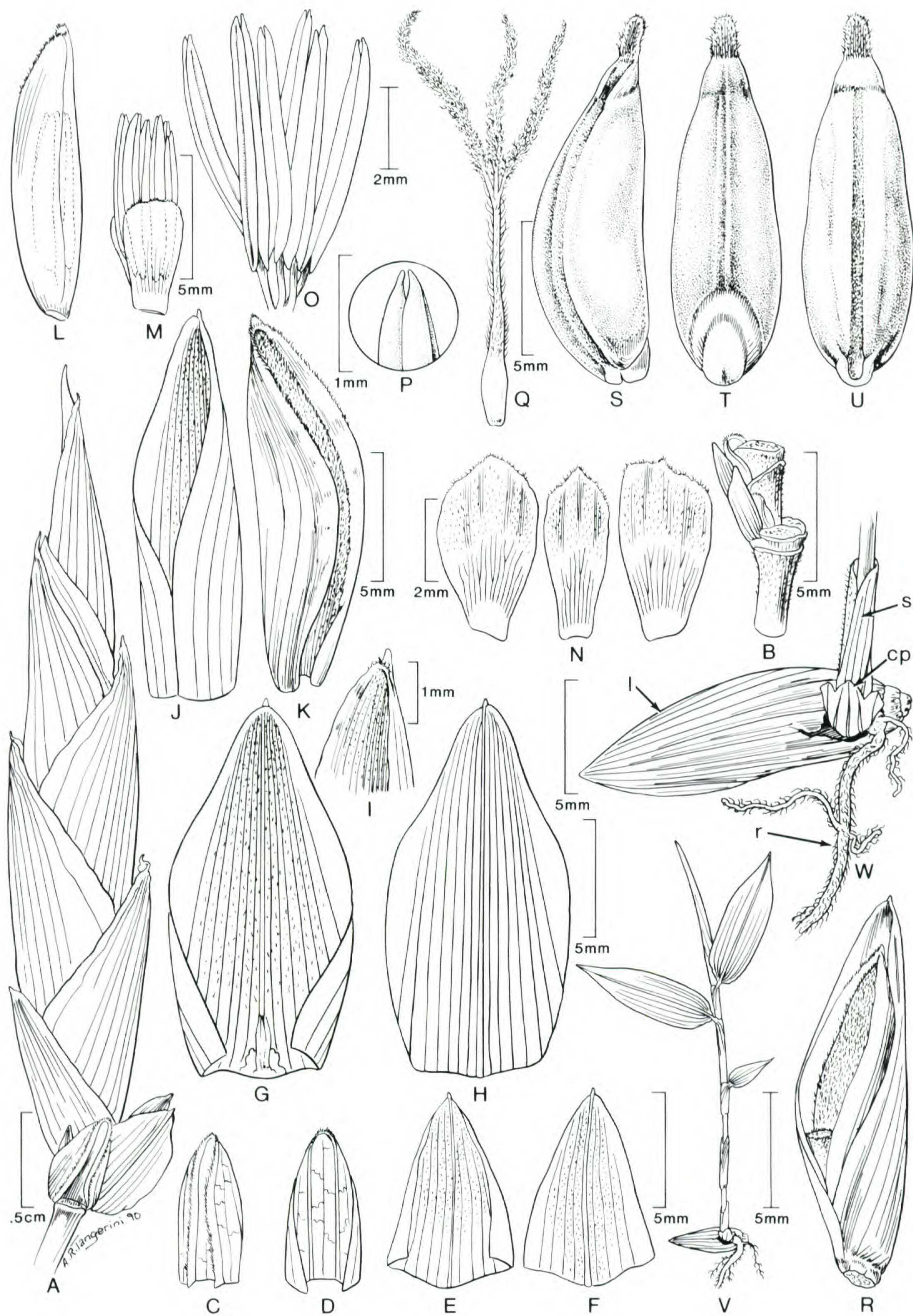


Figure 2. *Guadua chacoensis*. —A. Pseudospikelet showing prophyll, basal bracts, and florets. —B. Rachilla segment. —C. Prophyll, dorsal view. —D. Prophyll, ventral view. —E. Basal bract, ventral view. —F. Basal bract,

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dorsal view. —G. Lemma with a rudimentary palea below, ventral view. —H. Lemma, dorsal view. —I. Apex of lemma showing mucro and ciliate margin. —J. Palea, ventral view. —K. Palea showing the ciliate winged-keels, dorsal view. —L. Young palea enclosing androecium and gynoecium. —M. Young androecium and gynoecium protected by lodicules. —N. Lodicule complement. —O. Androecium with 6 stamens. —P. Anther apex. —Q. Gynoecium with 3 plumose stigmas. —R. Mature floret enclosing fruit with rachilla attached to the basal point. —S. Fruit with a short stylar column, lateral view. —T. Fruit showing the prominent embryotegium, ventral view. —U. Fruit showing the hilum, dorsal view. —V. Seedling showing the germinated caryopsis. —W. Detail of the basal portion of seedling showing the lemma attached to the fruit (l), the coleoptile (cp), the first basal culm-leaf sheath of the primary shoot (s) and the root (r). Based on: A-Q, *Quarin 3210*; R-U, *Quarin et al. 1859*; V, W, *Krapovicas et al. 23851*.